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# STRUCTURAL RELATIONS IN XENOPARASITISM

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AT various times normally independent plants have been experimentally caused to grow and develop within the tissues of other independent plants, deriving from this arrangement food and food-materials and organizing tissues and organs.<sup>1</sup> Although in themselves short-lived, the artificial parasites offer interesting suggestions as to the possible conditions under which true parasitism may arise in nature.<sup>2</sup> It is clear, for instance, that the mutual relation of parasite and host is extremely complex, both from a purely physiological point of view and from a structural one. On the one hand, it presupposes suitable osmotic relations and not unfavorable chemical reactions, and on the other, among other things, the fitting and exact adjustment of the tissues of the parasite, and it signifies atrophies as well.

When we observe the leading structural changes which normally occur in the growth of a haustorium of a habitual parasite, such, for example, as the mistletoe,<sup>3</sup> we find a course of development which is full of suggestions. A young haustorium is composed mainly of undifferentiated ground tissue, but there are the beginnings of conductive tissue within, and a protective epidermis without. Upon the commencement of the parasitic relation the most marked changes occur. In the first place epithelial cells

<sup>1</sup> "Artificial Parasitism, etc.," G. J. Peirce, *Bot. Gaz.*, **38**: 214, 1904. "The Condition of Parasitism in Plants," D. T. MacDougal and W. A. Cannon, Publ. No. 129 Carnegie Inst. of Wash., 1910. "An Attempted Analysis of Parasitism," D. T. MacDougal, *Bot. Gaz.*, **52**: 249, 1911.

<sup>2</sup> "An Attempted Analysis of Parasitism," D. T. MacDougal, *Bot. Gaz.*, **52**: 249, 1911.

<sup>3</sup> "The Anatomy of *Phoradendron villosum*," W. A. Cannon, *Bull. Torr. Bot. Club*, 1901.

are formed directly from parenchyma, and then after penetrating the host, such of the periphery of the haustorium as touches non-living cortical host cells, organizes cork. Finally, upon the attainment by the haustorium of the woody cylinder the conductive tissue of the haustorium opposes cell for cell the conductive tissue of the host, and in such parasites as possess sieve-tubes, the sieve-tubes hold a similar relation to the sieve-tubes of the host.<sup>4</sup> It happens therefore in habitual parasites that a portion of the development of the haustoria occurs after the parasitic relation has been entered into, so that the direction of the development of much of the tissue of the haustorium is fortuitous, depending in part on the position occupied by the tissues of the host.

#### DURATION OF THE XENOPARASITIC RELATION

Although induced parasitism means naturally a limited period during which the artificial relation can be continued, this period varies greatly with the different nutritive couples. A review of this phase of the subject will not be given here, as it is completely presented in the papers referred to above, but two or three of the most pertinent parasitic relations will be cited. Peirce grew *Pisum sativum* on *Vicia Faba* to maturity (Peirce, "Artificial Parasitism," *l. c.*). MacDougal (see above) records many experiments of which the following may be given: *Cissus laciniata* was grown on *Opuntia blakeana* from February 1, 1908, until April 19, 1909, and another culture, which is especially treated in this paper, lasted from early autumn, 1911, to June 10, 1912. In the instances where *Cissus* was employed roots were freely formed, the stem attained considerable length and organized tendrils and leaves. From these facts a large capacity for adjustment on the part of the induced parasites is exhibited, and also a degree of physiological adaptability is shown which reveals something of the plasticity of such plants and argues a fair suitability for the dependent relation.

<sup>4</sup>"On the Structure of the Haustoria of Some Phaneorgamic Parasites," G. J. Peirce, *Ann. Bot.*, 7: 324, 1893.

XENOPARASITISM OF *CISSUS LACINIATA*

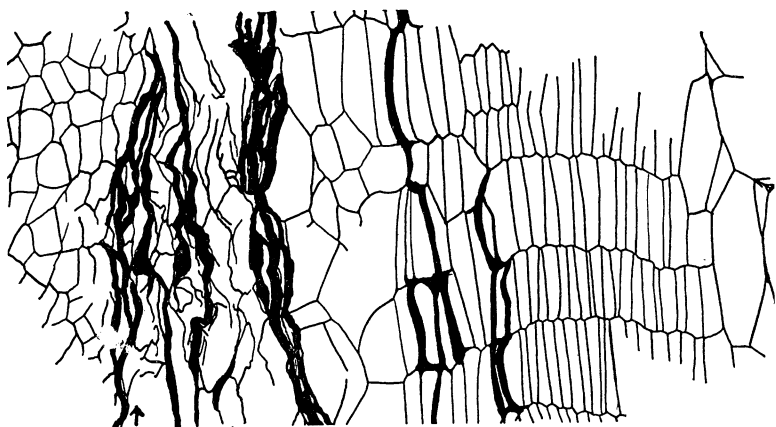
The induced parasite *Cissus laciniata* exhibits in the structure and form of its roots (the shoot was not studied) certain deviations from the normal which are of significance and interest. A history of the experiments in which this species was used as a parasite is given in another place, suffice it to state here that a cutting of the Mexican grape (*Cissus laciniata*) was introduced into the tissues of *Opuntia blakeana* and allowed to remain several months. A shoot with leaves and tendrils was formed. After the culture had been running some time a root of the grape was seen to emerge from the surface of the cactus, to grow downwards, and to penetrate the soil. It was severed so that the *Cissus* had connections with the cactus only. On June 10, 1912, the newly organized leaves were seen to be relatively small and the tendrils not to develop. The culture was thereupon taken down and the roots of the parasite dissected out so that their relations to the host tissue might be learned.

All of the roots of *Cissus* which were situated within the tissues of the cactus were found to be fleshy. A main root was traced from the base of the cutting through the tissues of the cactus for a distance of 3 cm. when, as above mentioned, it issued from the cactus and found its way into the soil. This root gave off one branch about 1 cm. from its point of origin, which extended for a distance of 3 cm. into the tissues of the cactus. The root last mentioned gave rise in turn to a branch which attained a length of 1.5 cm. In addition to these roots there were several short ones which reached little beyond the surface of the parent root. All roots except the one especially mentioned as not behaving in this manner were wholly enclosed within tissues of the host.

## STRUCTURE OF FREE-LIVING ROOTS

The portion of the roots which are free-living offer useful points of comparison, for which purpose the anatomy will be briefly reviewed.

A root 2.0 mm. in diameter shows the usual divisions into central cylinder and cortex. The endodermis is well marked. The epidermis is discolored and bears the remains of root-hairs. Cork has not begun to form, however. The cortex is composed of cubical parenchyma; the parenchyma of the central cylinder offers no unusual features. Little starch or crystals are to be seen.



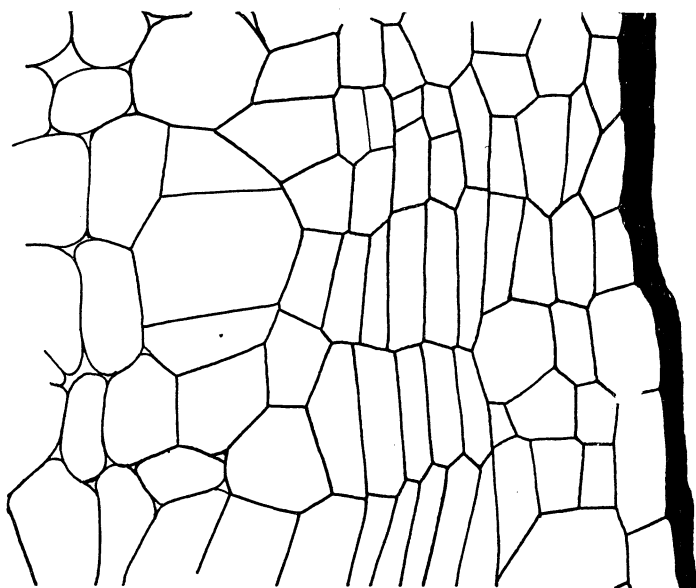
ANATOMICAL RELATION OF THE *Cissus-Opuntia* COUPLE. On the left appears the extra-cortical portion of the root with the limit indicated by the arrow. On the right is the wound tissue of the cactus, and between this and the root lies disorganized cactus cells.

### STRUCTURE OF THE PARASITIC ROOTS

The roots of *Cissus*, which developed within the tissues of the cactus, varied in diameter from 2 to 5 mm. and showed characteristics which were in certain regards quite different from those of the free-living roots examined.

If a cross-section of a root 2 mm. in diameter is studied the usual differentiation into cortex and central cylinder will be noted. The cortex is composed of relatively large cells a few of which contain stellate crystal aggregates and raphides. A layer of cork, over half dozen cells in thickness, bounded by the dead remains of the epidermis,

lies on its periphery. The remains of root-hairs were looked for but were not found. A well defined endodermis with granular contents, a portion of which is starch, limits the cortex on its inner surface. The central cylinder has relatively wide medullary rays and a large pith containing much starch. Opposite each



CROSS-SECTION OF PARASITIC ROOT OF *Cissus laciniata* SHOWING THE FORMATION OF CORK AND THE DISORGANIZED EPIDERMIS.

bundle, and about 2 cells inside the endodermis, there is a plate which may be composed of leptome, and which in some favorable material appears to be thickened wall only.

A root 5 mm. in diameter has essentially the same structure as the smaller one above described. The main differences lie in the heavier cork and the thicker cortex. The plate which lies opposite each fibro-vascular bundle, also, is heavier. The endodermis is noticeably poorer in starch.

## TISSUES OF THE HOST

The structure of the flat stems of *Opuntia*, broadly speaking, consists of thin-walled, large parenchyma, through which there course strands of conductive tissue. Protection of the stem is afforded by a heavy cuticularized epidermis.

When the parasitic relation is entered into, wound tissue, with heavy outer walls in certain cells similar to those of the cork, is formed about the injury caused by the introduction of the cutting. The cutting sends out adventitious roots which penetrate the parenchymatous tissue of the host, and sooner or later these roots are surrounded by wound tissue which the host promptly organizes as a result of the unusual stimulation. By this formation the water-storing ground tissue of the host is separated from the living cells of the parasite.

## TISSUE RELATIONS OF PARASITE AND HOST

In rapidly growing roots, contact is made with the living parenchyma of the cactus, and the parasite is in physical position to absorb foods and food materials. In instances, however, where root growth is slow, wound tissue is formed by the cactus, and the parasitic relation is not favorable for absorption. Following the formation of wound tissue cork is organized by the parasite, so that the cushion of non-living material separating host and parasite in the older portions of the culture, comes to be derived from both species.

When one compares the structural relations of a haustorium of a habitual parasite with the analogous absorbing organ of such a xenoparasite as *Cissus*, several suggestive inferences may be derived. The relation may be presented briefly in the following parallel:

<i>Xenoparasite</i>	<i>Parasite</i>
No special digestive cells.	Epithelium developed.
Root-hairs suppressed.	No root-hairs formed.

Foods and food materials enter haustorial root through epidermis.

Cork formed after establishment, following organization of wound tissue by host.

Tissues articulate with the corresponding host tissues.

Meristematic tissue localized.

Foods and food materials enter haustorium through parenchyma, sieve-tubes, and vessels.

Terminal portions at least of all permanent tissues formed after establishment.

The same.

Meristematic tissue not localized.

The parallel given above suggests, as intimated in another paragraph, that any species which is to become dependent on another species possesses to a large degree the power of adaptability and morphological plasticity, so that the direction of the development of its tissues or organs can to a degree be modified. Atrophies result, and the assumption of unaccustomed functions, and tissues are organized in harmony with tissue formation, or other physiological activity on the part of the host.